On a new terrestrial genus and species of Scottiinae (Crustacea, Ostracoda) from Australia, with a discussion on the phylogeny and the zoogeography of the subfamily

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Abstract

The Scottiinae, thus far comprising the genera \textit{Scottia} and \textit{Mesocypris}, form an important lineage of (semi-) terrestrial ostracods within the family Cyprididae. \textit{Scottia} has a mainly Holarctic distribution, while \textit{Mesocypris} was thus far known from Australia (including Tasmania) and Africa (including Madagascar). Detailed description of a new species from Australia and subsequent cladistic analysis of the Scottiinae as a whole, based on morphological characteristics, showed that the two geographically separated clusters of \textit{Mesocypris s.l.} actually belong in two genera. The most derived Australian clade requires the erection of a new genus. \textit{Austromesocypris} n.gen., and its type species, \textit{A. berentsae} n.sp. are here described. \textit{Austromesocypris} n.gen. and \textit{Mesocypris s.s.} are lodged in the tribe Mesocypridini, previously a subfamily synonymised with Scottiinae, but here re-instated with a change of rank, while \textit{Scottia} is in the nominate tribe Scottiini. Various morphological transformation series are present in the Mesocypridini, i.e. progressive loss of natatory setae on A2 and fusion of segments on A1. The latter transformation is a reversal to aspects of juvenile morphologies through heterochronic processes. Analysis of all aspects of the A1 chaetotaxy, by comparison to an ontogenetic sequence of another cypridinid, shows that evolution of different characters (e.g. segment fusion and number and position of setae) has occurred independently.

The distribution of the Scottiinae in the southern Hemisphere is briefly discussed in light of past continental distributions.

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Keywords: \textit{Austromesocypris}; Taxonomy; Semi-terrestrial species; Phylogeny; Zoogeography; Gondwana

Introduction

Species of podocopid ostracods have abounded in both marine and freshwaters since the early Palaeozoic. However, several lineages have proliferated in (semi-) terrestrial environments, for example in Darwinulidae, Terrestricytheridae, Candoninae, Cypridopsinae and Scottiinae. Especially, the latter lineage is highly adapted to such environments. It is also in this group that the first truly terrestrial ostracod, \textit{Mesocypris terrestris}, was discovered in the South African Knysna forest (Harding 1953). Previous findings of a species of this genus (\textit{M. pubescens}) in various parts of Kenya had

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been restricted to semi-terrestrial conditions (e.g. mosses, splash zones of a water fall, etc.) (Daday 1908, 1910; Klie 1939). After that, Chapman (1960, 1961) described Scottia audax and S. insularis, while Schornikov (1969) reported on Terrestriocythere pratensis. Four seminal papers on terrestrial ostracods appeared in the 1980s: Schornikov (1980) described several new species and genera from the Far East and from a Pacific Island, De Deckker (1980, 1983) described terrestrial ostracods from Australia and Tasmania and Danielopol and Betsch (1980) reported on terrestrial Mesocypris and a candonid from Madagascar.

Recently, the taxonomic and evolutionary interest in these lineages was again revived. The compilation of a checklist of non-marine ostracods of South America (Martens and Behen 1994) revealed that no terrestrial ostracods at all had been reported from this continent and this prompted the lab of Prof. Carlos da Rocha (University of São Paulo) to start a project on the terrestrial crustacean fauna of São Paulo State. The presence of a rich variety of (semi-) terrestrial ostracods was established and these are at present being described (Pinto et al. 2003, 2004, in press). Matzke-Karasz (1995) provided detailed descriptions of several species of Scottiinae, using both classical and new anatomical features, while Smith et al. (2002) described a new species of Scottia from Japan and provided a key to the species of the subfamily.

As a result of these various reports, a confusing picture on the evolution of terrestrial ostracods appeared. Not only did these faunas consist of several, unrelated lineages, their distribution was also often enigmatic. For example, the fact that Mesocypris s.l. occurs in Australia and Africa, but not in South America, provides an unexpected zoogeographical scenario. New material of a species of Mesocypris from an Australian rainforest and subsequent phylogenetic analysis of the entire genus showed the existence of two lineages, one in Australia and one in Africa. Austromesocypris n.gen. is here described to comprise the Australian species, including its new type species, A. berentsae n.sp. Several character transformations within this clade, one through heterochronic development, are discussed.

Material and methods

Material

Material for the present study was collected during a fieldtrip to The Barrington Tops forest in New South Wales, Australia in February 2001. Several biotopes in the forest were sampled, e.g. mosses in splash zones of waterfalls, littoral areas of streamlets, etc., but only leaf litter in the forest itself yielded specimens of Mesocypridini. The species is thus genuinely terrestrial. This material is here extensively described, as it belongs to a new genus and species. Comparisons with other species of Mesocypridini and of the sister genus Scottia were performed using descriptions in the literature; especially, in Daday (1910), Harding (1953), Danielopol and Betsch (1980), De Deckker (1980, 1983), Matzke-Karasz (1995) and Smith et al. (2002). The New Zealand species Scottia insularis Chapman, 1963, although potentially of high phylogenetic and zoogeographical significance, is too incompletely described to be incorporated in any analysis. Nevertheless, the presence of Scottia in both Australia and New Zealand, away from it congeners in the northern Hemisphere, deserves further investigation.

Phylogenetic analysis

A phylogenetic analysis of the subfamily Scottiinae was performed based on 21 morphological characters (see Appendix A), using the herpetocypridinid ostracod species Psychrodromus olivaceus as outgroup (based on internal anatomy of the hemipenis, the Herpetocypridinae are thought to be a closely related subfamily to Scottiinae within the Cyprididae). All characters that were thought to carry phylogenetic signal were included; limitations were posed by the original descriptions of the species for which no material was available. The data matrix (see Appendix B) was analysed using PAUP 4.06 (Swofford 1998). Input order of taxa was as in the matrix in Appendix B. Characters 3, 4 and 15 were allocated a weight of 10 (default = 1), as fusion and division of segments was deemed to carry a heavier phylogenetic signal than, for example, features of setae and claws. All characters were allocated the type ‘ordered’ (Wagner parsimony). Trees were built using maximum parsimony (MP) with the branch-and-bound routine (furthest taxon input) and with neighbour joining (NJ) methods. Bootstrapping used the full heuristic method in MP, and character weighting option 3 (repeat counts treated as integer values); for both MP and NJ bootstrapping, 10,000 replicates were performed.

What are terrestrial ostracods?

Schornikov (1980) argued that he did not consider his ostracods from terrestrial habitats themselves to be terrestrial, because these animals gather a film of moisture around and within their valves, so that they still breath through water. We reject this point of view, as nearly all forms of animal respiration, even that of humans, requires a degree of moisture, either externally or internally (within lungs). When animals live in
terrestrial conditions, i.e. outside of free standing or flowing water, we consider them terrestrial.

**Abbreviations used in text and figures**

<table>
<thead>
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<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>A1</td>
<td>Antennula</td>
</tr>
<tr>
<td>A2</td>
<td>Antenna</td>
</tr>
<tr>
<td>Cp</td>
<td>Carapace</td>
</tr>
<tr>
<td>H</td>
<td>Height of valves</td>
</tr>
<tr>
<td>L</td>
<td>Length of valves</td>
</tr>
<tr>
<td>LV</td>
<td>Left valve</td>
</tr>
<tr>
<td>Md</td>
<td>Mandibula</td>
</tr>
<tr>
<td>Mx1</td>
<td>Maxillula</td>
</tr>
<tr>
<td>ns</td>
<td>Natatory setae</td>
</tr>
<tr>
<td>R</td>
<td>Rome organ</td>
</tr>
<tr>
<td>RV</td>
<td>Right valve</td>
</tr>
<tr>
<td>T1</td>
<td>First thoracopod</td>
</tr>
<tr>
<td>T2</td>
<td>Second thoracopod</td>
</tr>
<tr>
<td>T3</td>
<td>Third thoracopod</td>
</tr>
<tr>
<td>CR</td>
<td>Caudal rami</td>
</tr>
<tr>
<td>S_a</td>
<td>Anterior seta of caudal rami</td>
</tr>
<tr>
<td>S_p</td>
<td>Posterior seta of caudal rami</td>
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Chaetotaxy of the limbs follows the model proposed by Broodbakker and Danielopol (1982), revised for the A2 by Martens (1987). Higher taxonomy of the Ostracoda follows the new synopsis by Horne et al. (2002).

**Results**

**Taxonomic descriptions**

**General**

<table>
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<th>Author</th>
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<tr>
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<td>Podocopa Müller, 1894</td>
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<td>Order</td>
<td>Podocopida Sars, 1866</td>
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<tr>
<td>Superfamily</td>
<td>Cyprididea Baird, 1845</td>
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<tr>
<td>Family</td>
<td>Cyprididae Baird, 1845</td>
<td></td>
</tr>
<tr>
<td>Subfamily</td>
<td>Scottiinae Bronstein, 1947</td>
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</table>

**Austromesocypris n.gen.**

Type species. *A. berentsae* n.sp. (here designated).

Diagnosis. Cp small to medium-sized ($L = 0.5$--$0.9$ mm), oviform, dorsally arched and ventrally flattened, smooth and often hirsute, especially in the ventral area. Central muscle scars a vertical row of three rectangular scars and a smaller one below plus 2 other scars posterior to that row. Calcified inner lamellae wide. Claws on all appendages short and strongly chitinised. Natatory setae on A2 strongly reduced. CR symmetrical or asymmetrical, with shaft and claws short and stout, attachment simple.

**Tribe Mesocypridini Hartmann and Puri, 1974 (change of rank)**

Diagnosis. Carapace smooth or pseudo-punctate, often strongly pilose, mostly elongated and with width less than half of the length. LV/RV overlap occurring at anterior, ventral and posterior sides, sometimes also along dorsal side. Both LV and RV with inner lists on well-developed calcified inner lamellae; selvages present or absent.

A1 with segments 4 and 5 and 6 and 7 either fused or separated. A2 with 2--6 short natatory setae. T2 with segments 2 and 3 (completely or incompletely) fused; 4th segment with subapical seta short, mostly 1/3 or 1/4 of length of end claw (1/2 in *M. pauliani*); setae e and f mostly short (long in *M. terrestris*). CR asymmetrical, right ramus with proximal seta a thick claw and with shaft strongly denticulate, left ramus with proximal seta a more slender claw and with shaft finely pectinate.

Differential diagnosis. The new tribe differs from the nominal Scottiini (which comprises *Scottia* as single genus) mainly in the shape of the valves (more rounded and wider in Scottiini), the fused segments 2 and 3 of the T2 (separate in Scottiini) and the length of the subapical seta h3 on the terminal segment of T2 (short in Mesocypridini, long and claw-like in Scottiini).

Remarks. Hartmann and Puri (1974) erected the Mesocypridinae within the Cyprididae to comprise the genus *Mesocypris*. This subfamily was later synonymised with the Scottiinae, but the present discovery that the latter subfamily consists of two separate lineages (see discussion) allows the re-establishment of the Mesocypridini as a tribe within the Scottiinae. The genus *Scottia* is then automatically allocated to the nominal tribe, Scottiinae.
Differential diagnosis. *Austromesocypris* n.gen. differs from *Mesocypris Daday*, 1910 mainly in soft part features. Whereas all segments of A1 are separated in *Mesocypris* s.s., there is a progressive incidence of fused segments in the A1 (either through heterochrony, segments fail to separate during ontogeny, or through secondary fusion — see discussion) in *Austromesocypris* n.gen., with segments 4 and 5 being fused in all three species allocated to this genus and with segments 6 and 7 fused in *A. berentsae*, partly fused in *A. australiensis* and separate in *A. tasmaniensis*. Other differences are in the number of ns on the A2, which is more reduced in *Austromesocypris* n.gen. (2 short setae in all three species, 4-6 in *Mesocypris* s.s.), and in the reduction of seta h3 in T2 (ratio with apical claw is 4.8-8 in *Austromesocypris* n.gen., 2-3.7 in *Mesocypris* s.s.).

Differences in valves are somewhat uncertain, due to incomplete descriptions. *Austromesocypris* n.gen. lacks selvages in both valves, but has prominent inner lists, while at least *Harding* (1953) reports the presence of strong (even crenulated) selvages in the African *M. terestris*. *De Deckker* (1983) reported submarginal selvages in *M. australiensis*, but the illustrations only show inner lists. It is here postulated that the (African) *Mesocypris* species have strongly developed selvages, while the Australian species of *Austromesocypris* lack these structures. However, the validity of this character remains to be confirmed.


*Austromesocypris berentsae* n.sp.


Type locality. Leaf litter, Barrington Tops, Chichester, Jerusalem Creek, New South Wales, Australia (coordinates: 32° 14’ 5” S, 151° 43’ 38” E), coll. 22.02.2001 by Penny Berents, Giampaolo Rossetti, Isa Schön and Koen Martens.

Type material. **Holotype;** female (no. p.68089(GR.497)): soft parts dissected in glycerine in a sealed slide, valves stored dry in a micropalaeological slide. **Paratypes:** one female dissected and stored as the holotype (no. p.68090(GR.496)), five females stored in toto dry in micropalaeontological slide after use for SEM (nos p.68091(GR.498,499,503-505)); c 10 females stored in toto in 80% alcohol (no numbers).

Repository. The holotype and six paratypes are deposited in the Crustacea collections of the Australian Museum (Sydney, Australia); other paratypes are in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium).

Etymology. The new species is named in honour of Dr. Penny Berents, in acknowledgement of her significant contributions to the study and conservation of Australian aquatic invertebrates and in gratitude for her assistance in the collection of the material described here.

Diagnosis. Small species (*L = c 550 μm*), with elongated carapace (*L/H > 2*), segments 4 and 5 and 6 and 7 of A1 completely fused, 2 natatory setae, 3 t-setae, 2 z-setae and length of claw GM about twice the length of Gm on A2, a short seta h3 on T2 and a long proximal seta on the CR.

Description of female. Cp elongated in lateral view, dorsal margin evenly rounded, with highest point situated in the middle; both anterior and posterior margins rounded, slightly produced towards the ventral side; the latter slightly sinuous (Fig. 1I). In dorsal view (Fig. 1J), with lateral sides nearly straight and parallel, greatest width situated in the middle, anterior and posterior edges bluntly pointed, hinge line not straight, middle part convexly curved towards the left side; LV overlapping RV on all sides. External valve surface densely set with long and stiff setae, especially along the ventral margin (Figs. 1K,M).

LV internally with both anterior and posterior calcified inner lamella well-developed, anteriorly with two sub-parallel inner lists, in between of which pronounced, oblique striae occurring; posteriorly with large inner list, not parallel to valve margin, nor to inner margin; both valve and inner margins forming accentuated ridges along the entire circumference (Figs. 1A–C).

RV also with well-developed calcified inner lamellae, anteriorly with two weak inner lists, without oblique striae, posteriorly with two inner lists, running parallel to inner margin; valve margin simple, not ridge-like, inner margin ridge-like, especially anteriorly (Figs. 1D–F).

A1 5-segmented, both segments 4 and 5 and 6 and 7 fused (Figs. 2A and 5A,B). First segment (constituting of fused segments 1 and 2) dorsally with one short, basal seta and 2 long, apical setae. Second (3) segment with one dorso-apical seta and one ventro-apical Rome, the latter forming a short conical tube. Third segment (4 + 5) dorsally with one short, subapical seta, and two long apical ns, ventrally with one short plumous seta. Fourth segment (6 + 7) with one long, medio-dorsal ns, one short dorsa-apical seta and 2 long, medio-apical ns. Fifth (8) segment with 2 long ns, one shorter seta and one aesthetasc Ys, about 4/5 of the length of the short seta.

A2 with stout and hirsute appearance (Fig. 2B). First segment subapically with a row of spiny pseudochaetae, a ventro-apical seta of medium-length, and a plate-like exopodite, bearing one long seta, hirsute in its distal
half, a short seta with swollen base and whip-like distal half and in between with one plumous seta (Fig. 5E).

Second segment (first endopodal segment) with several rows of spiny pseudochaetae, a ventral aesthetasc Y, inserted slightly over half the length of the ventral margin, with distal part swollen (Figs. 5G,H) and with
two short ns (not reaching edge of segment) (Fig. 5H). Third segment (second endopodal segment) medio-ventrally with 3 t-setae (Fig. 5F), one shorter, hirsute, two longer, and aesthetasc y₁, medio-dorsally with 2 subequal setae; apically with 2 z-setae (Fig. 5C), one short, stout claw G₂ (see remarks), a long claw G₁, a slightly shorter claw G₃ and aesthetasc y₂. Terminal segment (Fig. 5D) with claw G₃ reaching beyond the tip of claw G₃, but not as far as the tip of G₁; Gₐ a seta, with slightly swollen base and hirsute distal half; aesthetasc y₃ shorter than accompanying seta; seta g missing.

First segment of Md-palp dorsally with respiratory plate, ventro-apically with two hirsute s-setae and the alpha-seta, the latter with swollen base and smooth, pointed tip. Second segment with three subequal, hirsute setae in dorso-medial to dorsal-apical position, ventrally with four long and one shorter setae, all hirsute, beta-seta short, tapering and hirsute in distal half. Third segment medially with a row of long and stiff pseudochaetae, dorsally with three subequal, subapically inserted setae, medio-apically with a relatively short gamma-seta, ventrally with one long and one short setae subapically inserted. Terminal segment
with three claws, two long, one shorter and two short setae (Figs. 3A and 4C).

Mx1 with first palp-segment carrying four apical setae, three long, one shorter, all hirsute. Second palp-segment rectangular, almost twice as long as basal width, apically with four setae of varying length. Third endite with two smooth Zahnborsten and seven setae, three short, four long. First endite with several apical setae, two of which long (about twice as long as others) and hirsute (Fig. 2D).

T1 with large, swollen palp, apically with three setae, one long central and two shorter lateral, all set with long setulae. Two a-setae short, setae b and d long and hirsute; endite apically with c 7 setae of varying length, most hirsute (Fig. 2E).

T2 a walking limb (Fig. 2C), seta d1 absent, d2 of medium length. Penultimate segment fused, elongate, with apical seta g plumose (Fig. 4F); setae e and f short, hirsute (Fig. 5).

T3 a cleaning limb, with setae e and f short and hirsute (Figs. 3B and 4D,E).

CR asymmetrical, but both with stout ramus and claws (Fig. 4G). Left ramus (Fig. 3C) apically curved to the ventral side, both ventral and dorsal margin with rows of pseudochaetae, S_p short and hirsute, S_a long and hirsute, extending well beyond tip of largest claw; both claws set with a ventral row of teeth. Right ramus (Fig. 3D) distally curved towards the dorsal side, ventral margin of ramus set with a row of teeth, setae and claws as in the left ramus.

Male unknown.

Remarks
1. The short, apical claw on the second endopodal segment of the A2 is here called ‘G_2′, but could also be homologous with z_1; either of these structures is then missing.
2. Although many of the setae on various limbs are hirsute in this genus and species, it is noteworthy that atypical plumose setae (indicated by arrows in Fig. 2) occur on the third segment of the A1, the exopodite of the A2 and on the third segment of the T2 (seta g). The function of these special setae is unknown.

Measurements (in μm).  
RV: L = 520, H = 232.
Relationships. *A. berentsae* n.gen., n.sp. is most closely related to *A. australiensis* and *A. tasmaniensis*. As these species share a number of synapomorphic features, such as fused segments of A1, number of natatory setae on A2, etc., they were grouped in a separate genus. *A. berentsae* n.gen. n.sp. can nevertheless be distinguished from *A. australiensis* by the *L/H* ratio (>2 in *A. berentsae*, c. 0.7 in *A. australiensis*), by the presence of

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**Fig. 4.** *A. berentsae* n.gen., n.sp., female: (A) LV, internal view, central muscle scars (GR.499). (B) LV, internal view, detail posterior part. (C) Md-palp (GR.498). (D) T3 (GR.498). (E) T3, detail distal part (GR.498). (F) T2, detail penultimate and last segments (GR.498). (G) CR (GR.498). Scale = 83 μm for A, 93 μm for B, 77 μm for C, 114 μm for D, 17 μm for E, 15 μm for F, 93 μm for G.
Fig. 5. *A. berentsae* n.gen., n.sp., female (GR.498). (A) A1, medial view. (B) A1, detail fourth and fifth segments. (C) A2, detail second endopodal segment. (D) A2, detail terminal claws. (E) A2 exopodite. (F) A2, detail second and third endopodal segments. (G) A2, detail first and second endopodial segments, medial view. (H) A2, detail first and second endopodial segments, lateral view. Scale = 37 μm for A, 16 μm for B, 14 μm for C, 43 μm for D, F–H, 20 μm for E.
three short dorsal setae on the third segment of the Md-palp (4 in *A. australiensis*) and by the long proximal seta on the caudal ramus (spine-like in *A. australiensis*), amongst other details in chaetotaxy. The new species is even more closely related to *A. tasmaniensis*, from which it can mainly be distinguished by the fused segments 5 and 6 of the A1 (separate in *A. tasmaniensis*), the ratio between the length of the short seta on the 7th segment and that of the segment itself (0.7 in *A. berentsae* n.sp.; 1.6 in *A. tasmaniensis*) and the length of the dorsal setae on the 2nd segment of the Md-palp (long in *A. tasmaniensis*, short in *A. berentsae* n.sp.).

Ecology. In the type locality, the new species occurred in a fully terrestrial habitat, namely leaf litter in a temperate rainforest; the station where the specimens were collected was situated on a small hill, well away from any stream or water fall splash zone.

**Phylogenetic analysis of Scottiinae**

The MP (yielding a single most parsimonious tree) and the NJ analyses (Fig. 6) give similar topologies of the relationships between the extant species in the Scottiinae. Scottiini and Mesocypridini are two well-supported clades (bootstrap values 81 and 100 in MP, 75 and 100 in NJ, respectively). Within Mesocypridini, the Australian *Austromesocypris* n.gen. clade (with *A. australiensis*, *A. tasmaniensis* and *A. berentsae* n.sp.), is highly supported (bootstrap value = 100 for both MP and NJ) and is the most derived within the subfamily, as is best shown in the NJ tree. The African clade, *Mesocypris* s.s., is closest to the root. In the MP tree, *M. terrestris* is most basal, followed by *M. pauliani* and *M. madagascariensis*, respectively. In the NJ tree, the branching sequence of *M. pauliani* and *M. terrestris* is reversed. With the description of *Austromesocypris* n.gen., *Mesocypris* s.s. becomes a paraphyletic genus. In both MP and NJ trees, *S. pseudobrowniana* and *S. birigida* form a well-supported cluster (bootstrap values = 85 and 91, respectively), with *S. audax* being more distant from the other two species within the genus.

**Discussion**

**Morphological evolution of the Scottiinae**

The subfamily Scottiinae consists of two clearly separated clades, formalised in the two tribes Scottiini and Mesocypridini. Within Scottiini, the single genus *Scotta* appears to have retained the most plesiomorphic character states (separate segments in A1 and T2, symmetrical CR, 6 ns, etc.), although also some synapomorphic features occur, i.e. the long and claw-like seta h3 on T2. The NJ tree clearly shows that the Australian clade (*Austromesocypris* n.gen.) of the Mesocypridini is the most derived one, with the African species being the most ancestral.

Within Mesocypridini, several characters show important transformation series. These often coincide with geographical distribution (Fig. 7), with the African representatives having the most plesiomorphic character states, the Australian taxa (including *A. tasmaniensis*) showing the most derived states. For example, the African taxa of *Mesocypris* have 4–6 ns on the A2, but only two occur in all three Australian species of *Austromesocypris* n.gen. The latter is assumed to be the more derived state through progressive loss of setae. In the A1, segments 3 and 4 and 5 and 6 of the A1 are fully separated in the African species (*Mesocypris*); segments 3 and 4 are fused in all three Australian species, while segments 5 and 6 are fused in *A. berentsae* n.gen. n.sp., partly fused in *A. australiensis*, but still separate in *A. tasmaniensis* (see appendices A and B).

The evolution of the A1 segments within *Mesocypris* needs some elaboration, because the fused segments could be thought to represent ancestral character states, when compared to ontogenetic series. For this discussion, the morphology of the A1 in species of *Austromesocypris* n.gen is compared to the full ontogenetic series of the related species *Eucypris virens* (*Eucypridae*) (Smith and Martens, 2000). Following this model (Fig. 8), the situation in *A. tasmaniensis*, with segments 4 and 5 fused and 6 and 7 separate is representative of the ontogenetic stage A-3 (6th stage). The A1 of *A. berentsae* n.gen. n.sp. with both segments 4 and 5 and segments 6 and 7 fused represents the situation in juvenile stage A-4 (5th stage). The adult stage is the 9th juvenile stage, but the A1 with all segments separate already occurs in stage A-2 (7th stage). The heterochronic evolution of the A1 segmentation in Mesocypridini thus represents the adult stage in the African species (*Mesocypris*), stage 6 in *A. tasmaniensis*, in between stages 5 and 6 in *A. australiensis* (with partly fused segments 6 and 7) and stage 5 in *A. berentsae* n.sp. The similarity between the morphology of the A1 in adults of Australian *Austromesocypris* n.gen. species and in earlier juvenile stages of other Cyprididae is valid for the degree of fusion and separation of the segments. However, there is only partial congruence for the number of setae on those segments. Indeed, several setae present in the adult cypridid A1 are missing in the species of the Australian clade, especially in *A. berentsae* n.sp, but all adult *Austromesocypris*-species have more setae than the presumed corresponding juvenile stages in *E. virens*. This shows that evolution of each segment and of each individual seta must be viewed as an
Fig. 6. (A) Cladogram of Scottiinae, obtained with the programme PAUP. Single most parsimonious tree using branch and bound. Options: characters 3, 4 and 15 with weight ‘10’ (default = ‘1’); characters states are ‘ordered’. *P. olivaceus* was defined as outgroup. Bootstrap values are from 10,000 replicates, with branch and bound search, using character weighting option 3 (repeat counts as integers). (B) Phylogram of Scottiinae, from neighbor joining analysis in PAUP. Options as in the previous tree. Bootstrap values are from 10,000 replicates, using character weighting option 3 (repeat counts as integers).
independent process. This conclusion was already reached for the A2 ns of species in the cypridinid genus *Herpetocypris* by Gonzalez Mozo et al. (1996).

The sequence of progressive heterochrony of the A1 in the *A. tasmaniensis* — *A. australiensis* — *A. berentsae* n.sp. is not fully congruent with the topology of either the MP and the NJ trees, in which *A. australiensis* is most ancestral in the Australian clade, whereas *A. tasmaniensis* and *A. berentsae* n.sp. are most derived. This incongruence between clade and character evolution further confirms that characters can evolve independently from each other within a clade. In this particular case, it shows that the heterochronic evolution of the A1 segmentation was not necessarily the driver of speciation within the Australian *Austromeso-cypris* clade and that the heterochronic development might have occurred independently in the three species. The fact that it occurs in the most derived clade, however, indicates that the heterochronic development is actually a reversal. The A1 with fully separated segments thus constitutes the plesiomorphic state in this subfamily; the reversal to fused segments is a derived state (Fig. 8).

The reasons behind the heterochronic development of the A1 are most likely adaptive. The A1 is generally used for swimming in most Cypridoidea, and in terrestrial ostracods alters its function to crawling. Fusion of segments might strengthen the limb, making it better suited for crawling. As several species of Mesocypridini do not have such secondary fusion, the fused segments are indeed most likely adaptations, and not pre-adaptations. Note, however, that the ventral side of most segments is devoid of setae and this might argue against the fact that these limbs are modified for crawling. At least some setae would be expected on the ventral side of a crawling limb. Direct behavioural observation of crawling in this group will demonstrate exactly how the A1 is used.

A similar type of evolution has been described in at least one other group of terrestrial ostracods, namely in the genus *Terrestricypris* Schornikov, 1980, which has fused antenular segments, whereas these segments are separate in the sister genus *Terrestricandona* Danielopol and Betsch, 1980. According to Schornikov (1980), *Terrestricypris* was described on (A-1) juveniles. However, all Brazilian species belonging to this genus (Pinto et al. in press) also had only two claws on this segment, but several specimens were fully adult as they had a large egg in the carapace (egg:carapace ratio 1/3 to 1/4). We argue that Schornikov’s material also consisted of adults. This situation is presently being analysed using new terrestrial material from Brazil (Pinto et al. in press), but the parallel scenario in two terrestrial ostracod groups (Terrestricypridini and Mesocypridini) strengthens the adaptive value of this heterochronic evolution. More heterochronic and other types of morphological evolution are presently being discovered in the podocopid A1 (e.g. Namiotko and Danielopol...
(2001) for Cryptocandona), underlying the relevance of this limb for phylogenetic reconstructions in Crustacea in general and in podocopid ostracods in particular.

Taxonomic implications

As the three Australian species of Mesocypridini appear to be quite different from the African ones, they are here grouped in a separate genus. Unfortunately, this turns the African clade of Mesocypris into a paraphyletic taxon. Although this is generally to be avoided, we feel justified in doing so, because morphological segregation is strongly underpinned by geographical separation. The fact that some progressive evolution is apparent in Austromesocypris n.gen. (see above, fusion of segments 6 and 7 in A1) does not hamper the creation of the new genus, as several other features (e.g. number of ns on A2, fusion of segments 4 and 5) are shared by all Australian taxa.

Zoogeography of Scottiinae

The two tribes of the subfamily have different distributions. Scottiini are known from the Holarctic, i.e. North America (Külköylüoglu and Vinyard 2000), Europe and most of Siberia (Meisch, 2000). This is true for both recent and fossil species (see lists in Kempf 1980, 1997). The recent discovery of S. birigida in Japan (Smith et al. 2002) appears to bridge the gap between the Holarctic and the enigmatic occurrence of S. audax in Australia and New Zealand, although the latter species retains a somewhat isolated position within the genus, which can only be verified once the Australasian specimens are re-examined.

Mesocypridini, on the contrary, occur exclusively in parts of the southern hemisphere, Mesocypris in Africa (including Madagascar) and Austromesocypris n.gen. in Australia (including Tasmania). The absence of this lineage in South America and the western part of the Pacific (e.g. New Zealand) is surprising. Extensive recent collections in (semi-) terrestrial habitats in Brazil (Pinto et al. in press) yielded about a dozen ostracod species belonging to various lineages, but no Scottiinae were found. Africa and South America were already separated by the Albian (102 My ago), whereas by that time Australia and Antarctica were still joined (Veevers, 2000).

Within Australia itself, the distribution of the three Austromesocypris-species is not congruent with their phylogenetic affinities, as A. berentsae n.sp. is more closely related to A. tasmaniensis, than to A. australiensis, although both A. berentsae n.sp. and A. australiensis occur on mainland Australia whereas A. tasmaniensis is known from Tasmania only.

It is only through a reappraisal of past distribution of the southern continents that the biogeography of the Scottiinae can be better appreciated. First of all, the reconstruction of Gondwana over approximately 160 million years ago shows India and Madagascar still forming part of Gondwana with also Antarctica and Australia being part of this ‘super’ continent. Only the northeastern part of India was in contact with Western Australia, with the rest of India fitting along the western part of Antarctica (see Veevers, 1984, 2000 for more details). Thus, it is of no surprise to determine that Mesocypris and Austromesocypris are closely related despite the formal severance of India from Gondwana that commenced at 118 million years ago. Tasmania, on the other hand, despite the fact that it is separated today from the Australian mainland by the shallow Bass
Straits, is the geological continuation of the mainland and was also attached to Antarctica. The close link between *A. tasmaniensis* and *A. berentsae* is therefore of no surprise, but must be as ancient as when Bass Strait was dry in the Quaternary during periods of low sea levels, when climate would have been drier and colder and consequently, no rainforest would have covered part of the dry Bass Strait. The existence of rainforests there would have occurred during parts of the Tertiary, a time during which the migration of *Austromesocypris* could easily have occurred. Similarly, during the continuous climatic fluctuations so typical of the Quaternary Era, rainforests would have expanded and waned, thus forcing the terrestrial ostracods to follow the rainforest migrations. It is known that Barrington Tops during the last glacial maximum did not have a substantial rainforest (Sweller and Martin, 2001). Nevertheless, some patches of rainforest must have remained in depressions and along gullies in order to permit a re-vegetation of the area once the climate became wetter at the onset of the Holocene. Of major interest, however, is that rainforest was fully re-established at Barrington Tops only 6500 years ago (Sweller and Martin, 2001). The terrestrial ostracods would have been found in those refuge areas in waiting for more favourable climates to be restored. The same phenomenon must have applied to all terrestrial ostracod taxa along the eastern portion of Australia during the Quaternary climatic fluctuations. This pin points to the fact that terrestrial ostracods, like all other inhabitants of rainforests, must be well-adapted to migration and recolonisation.

The distribution of *Scottia* in Australia and New Zealand poses another geological challenge as New Zealand was also attached to Gondwana, but laid adjacent to eastern Antarctica where the Ross Sea occurs today (see Veevers, 2000) and was located further south than Tasmania along the Gondwana block. Hence, it is of no surprise that *Austromesocypris* is absent from New Zealand and yet *S. audax* occurs on both landmasses. The intellectual challenge is to explain how *Scottia* with an almost entirely Holarctic distribution has relatives in Australia and New Zealand. Note that *S. audax* is widespread along the southern end of the Eastern Highlands of Australia (De Deckker, 1983) and is found in the same habitat as *A. australiensis*. Obviously, further confirmation that the terrestrial ostracods *S. audax* definitely belongs to *Scottia* (with molecular analyses on specimens from both regions) is warranted before any other biogeographical implications can be envisaged.

Two further Australasian records of Mesocypridini are of interest. Firstly, Eagar (1969) reported a Pleistocene mummified ostracod from the Wairarapa district (New Zealand) and provisionally identified it as an early instar of *S. insularis* Chapmann. However, the specimen was badly preserved and any taxonomic identification remains most provisional. Secondly, De Deckker (1982) reported *Mesocypris* spec. (and provisionally referred it to *M. insularis* Chapmann) from Quaternary profiles at Pulbeena and Mowbray swamps (Tasmania). This species is highly arched, but the anatomy of the valve margins indicates that the Tasmanian fossils might belong to *Austromesocypris*, most likely to an–as yet undescribed species.

**Outlook**

The comparative analyses of the biology, phylogeny and distribution of the Scottiinae in general, and of the Mesocypridini in particular, offers exciting possibilities to contribute to a number of general evolutionary questions. For instance, whether or not (and in which way) the heterochronic development can be adaptive is a fundamental question that can be addressed by research of the Mesocypridini. Comparative behavioural research should show how the A1 is used in these terrestrial ostracods. Also, why is heterochronic development blocked in the more ancestral *Mesocypris* species, whereas this constraint appears to be released in the more derived *Austromesocypris*-species? A comparative analysis of the postembryonal ontogeny in both lineages could reveal the exact timing of this release. Finally, molecular analyses of representatives of both lineages of the Mesocypridini will test the present morphology-based phylogeny and might be able to offer absolute datings of the split between the two lineages, to show whether this event is congruent with the break-up of Gondwana, or if it occurred at a later date.

**Acknowledgements**

Dr. Penny Berents (Sydney, Australia) is gratefully acknowledged for scientific and logistic assistance during the fieldwork and for extensive hospitality during the stay in Sydney. Dr. Isa Schön (Brussels, Belgium) greatly assisted in the fieldwork and found the first specimens of this new species. She also assisted with the graphics of the trees. Dr. Dan Danielepof (Mondsee, Austria), Dr. Renate Matzke-Karasz (Munich, Germany), Dr. Isa Schön and Dr. Karel Wouters (Brussels, Belgium) read the manuscript and suggested improvements. Julien Cillis and Claudine Behen (R.B.I.N.Sc, Belgium) offered technical assistance with the S.E.M. micrographs and with the line drawings, respectively. The manuscript was largely written during a visit of GR to KM, financed by the EU Project ABC granted to the R.B.I.N.Sc.
Appendix A

List of morphological characters and character states used for the cladistic analyses of the Scottiinae.

1 Cp length: > 1.0 (0), between 0.8 and 1.0 (1), < = 0.8 (2),
2 Cp L/H: > 2.0 (0), between 1.8 and 2.0 (1), < = 1.8 (2),
3 A1 segments 4 and 5: separate (0), fused (1),
4 A1 segments 6 and 7 separate (0), fused (1),
5 A1 segment 7 ratio length of small seta versus length segment > 4.0 (0), between 2.0 and 4.0 (1), < = 2.0 (2),
6 A2 natatory seta: 6 (0), 5 (1), 4 (2), 2 (3),
7 A2 t-setae: 4 (0), 3 (1), 2 (2),
8 A2 z-setae: 3 (0), 2 (1),
9 A2 G_M > G_m: < = 1.8 (0), between 1.8 and 2.4 (1), > 2.4 (2),
10 Md palp seta teta: external (0), internal (1),
11 Md palp seta alpha: narrow (0), swollen (1),
12 Md palp segment two dorsal setae: three subequal (0), two long and one short (1),
13 Md palp segment three dorsal setae: four long (0), four short (1), three long (2), three short (3),
14 Md palp segment 4 setae: 4 (0), 3 (1), 2 (2), 1 (3),
15 T2 endopodite segments two and three: divided (0), incomplete (1), fused (2),
16 T2 apical claw h > h3: > 5.0 (0), between 2.0 and 5.0 (1), < 2.0 (2),
17 T2 setae g: 2 (0), 1 (1),
18 T2 length setae e, f: long (0), short (1),
19 CR: symmetrical (0), asymmetrical (1),
20 left CR S_e: > claws (0), < claws (1),
21 left CR S_p: very long seta (0), long seta (1), short seta (2), spine (3).

Appendix B

Matrix of morphological characters and character states used for the cladistic analyses in the present paper. P. olivaceus was used as outgroup, S. insularis was excluded from the analysis because more than half of the character states remain unknown in this species.

<table>
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<th>M. terrestris</th>
<th>M. pubescens</th>
<th>M. madagascariensis</th>
<th>M. pauliani</th>
<th>A. australiensis</th>
<th>A. tasmaniensis</th>
<th>A. berentsae</th>
<th>S. pseudobrowniana</th>
<th>S. insularis</th>
<th>S. audax</th>
<th>S. birigida</th>
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